Heterosis and Inbreeding Depression in Two Soybean Single Crosses

Joseph W. Burton* and Cavell Brownie

ABSTRACT

Heterosis is considered to be of little importance in soybean (*Glycine max* L. Merr.) because the crop is produced as "pure-line" cultivars or blends of inbred lines. The F_1 generations Holladay/Hutcheson (Cross 1) and Brim/Boggs (Cross 2) were generated by hand pollinations. Inbred generations were generated by bulk selfing. The F_1, F_2, F_3, F_4, and F_5 generations were yield-tested in replicated bordered single row plots in multiple years and locations. The average yield of Cross 1 F_1 was 16% greater than that of the highest-yielding parent and the average yield of the Cross 2 F_1 was 5% greater than the highest-yielding parent. Cross 1 showed significant inbreeding depression when regressed on percentage inbreeding which is clear evidence of dominance for yield. Possible genetic bases for heterosis in soybean include gene complementation or interaction of duplicate favorable loci in repulsion, linked dominant alleles that are inherited as a unit, a greater number of dominant alleles in the F_1 than either parent separately, multiple dosage-dependant regulatory loci, and/or overdominance. The existence of heterosis should be evidence that superior gene combinations are possible. The magnitude of yield heterosis may be a useful criterion for selection among biparental crosses.

H ETEROSIS generally is considered to be of little importance in soybean (*Glycine max* [L.]). A self-pollinated species, soybeans are produced as "pure-line" cultivars or blends of inbred lines. An efficient system for hybrid seed production on a commercial scale has not yet been realized. When yield heterosis has been measured in bordered row plots in more than one environment (of different studies), average high-parent heterosis has been reported as high as 20% (Palmer et al., 2001). Thus, significant yield increases appear to be possible with some F_1 hybrid combinations. The source of this heterosis is often thought to be effects of additive $\times$ additive epistasis that have been found in soybean breeding populations (Burton, 1987). Inbreeding depression (evidence for dominance effects) like heterosis is thought to be rare or nonexistent in soybean breeding populations (Pioneer Hi-Bred International, 1991).

Because most quantitative genetic studies have shown genetic variation for yield to be primarily additive (Burton, 1987), soybean breeders practice mostly pedigree selection, single seed descent (Brim, 1966), or some modification of those methods. Typically, a single cross between two good cultivars is followed by rapid inbreeding, derivation of F_4, F_5, or F_6 lines, line evaluation, and selection. In this process, the F_1 generation, which may be only three or four plants, is never com-

pared with succeeding generations. Thus, there rarely has been opportunity to observe or measure inbreeding depression where it would be most obvious, in F_2 performance compared with F_1 performance. In two studies where this was done, Brim and Cockerham (1961) and more recently Lewers et al. (1998), significant inbreeding depression was found. Brim and Cockerham worked with the parents and F_1 through F_5 generations derived from two single crosses, N48–4860 $\times$ 'Lee' and 'Roanoke' $\times$ Lee. In one case, the F_2 generation was 10% lower-yielding than the F_1 and in the other the F_2 was 11% lower than the F_1. Lewers et al. (1998) tested F_1 and F_2 generations and parents of six test crosses. The cultivar 'Harosoy' was the pollen parent for all six. Four of the six test crosses showed significant mid-parent heterosis in the F_1 generation. Two with significant mid-parent heterosis in the F_1 showed 11 and 16% yield declines in the F_2 generation.

The lines that Brim and Cockerham (1961) used to develop populations for their study were relatively unimproved and low yielding when compared with modern soybean cultivars, and Harosoy, used by Lewers et al. (1998), is in a similar category released in 1955. It may be that as yield improves with breeding in a self-pollinated species like soybean, and favorable genes accumulate, heterosis will decline. The objectives of the research reported here were (1) to estimate heterosis and inbreeding depression in populations derived from crosses between modern cultivars that would be typical of a standard pedigree selection program, and (2) to compare the results with those obtained by Brim and Cockerham (1961) and Lewers et al. (1998).

MATERIALS AND METHODS

The cultivars in this study were 'Holladay' (Burton et al., 1996), 'Hutcheson' (Buss et al., 1988), 'Brim' (Burton et al., 1994), and 'Boggs' (Boerma et al., 2000). Holladay (♂) and Hutcheson (♀) were cross-pollinated to generate one F_1 hybrid, hereafter designated Cross 1 and Brim (♀) and Boggs (♂) were crossed to generate the other, Cross 2. Holladay and Hutcheson were both of maturity group V and Brim and Boggs were both of maturity group VI. Thus, segregation for maturity among plants within each inbred generation was minimized.

Generating Hybrid and Inbred Generation Seeds

In 1998 and again in 2000, F_1 hybrid seed were generated by multiple hand pollinations over a period of 6 wk in the soybean nursery at Central Crops Research Station, Clayton, NC. The F_2 generation seeds were generated by self-pollination of ten F_1 plants in the 1998–99 USDA winter soybean nursery at Isabella, PR. In 1999, the F_1, F_2, and parents of the two crosses were field-tested in replicated trials. In 2000, the F_2 and F_3 generations and parents were tested using bulk-harvested seeds from 1999 F_1 and F_2 plots as the source of F_2 and F_3 generation seeds. In 2001, the F_1, F_2, F_3, and F_4 generations were field-tested along with parents. Bulk-harvested seeds

J.W. Burton, USDA-ARS, 3127 Ligon St., Raleigh, NC 27607; C. Brownie, Statistics, North Carolina State Univ., Raleigh, NC 27695. Received 9 Mar. 2006. *Corresponding author (joe_burton@ncsu.edu).

from F_2 and F_3 plots in 2000 were the source of F_3 and F_4 generation seeds. The F_2 generation seeds were generated from ten F_1 plants grown in the 2000–01 winter nursery. In 2004 tests, bulk-harvested seed from the F_2, F_3, and F_4 generations were used as the source of seeds for the F_3, F_4, and F_5 generations. Source of seeds for the F_2 was a remnant of F_2 seeds produced in the 2000–01 winter nursery.

Field Testing

Parents, F_1, and inbred generations were tested in three row plots. Rows were 0.96 m wide and 5.8 m long. At maturity, 0.5 m was trimmed from the end of each middle row before harvest. Only the remaining portion of the center row was harvested. When the F_1 generations were tested, F_1 seeds were planted only in the center row of the three-row plot and a blend of parents or F_2 seeds were planted in the rows on either side as borders. The materials were grown in a randomized complete block design with three replications (blocks) per location.

All tests were conducted on research stations in North Carolina. Tests were grown at the Central Crops Research Station, Clayton, NC in 1999, 2000, 2001, and 2004. In 1999 and 2004, those tests were grown on a Norfolk loamy sand (typic Paleudults) soil and on a Dothan loamy sand (plinthic Paleudults) soil in 2000 and 2001. Tests were grown at the Tidewater Research Station, Plymouth, NC in all 4 yr on a Portsmouth (typic Umbraquult) soil. In 1999, the test was also grown at the Sandhills Research Station, Windblow, NC on Fuquay sand (arenic Plinthic Kandiudults). Tests were grown at the Horticultural Crops Research Station, Clinton, NC in 2000 on an Orangeburg loamy sand (typic Paleudults) soil and in 2001 on a Norfolk loamy sand (typic Paleudults). Standard soybean production practices were applied to all tests plots. Irrigation was applied as needed at the Clayton and Windblow locations.

Statistical Analyses

For each type of cross, a mixed model analysis of variance (ANOVA) was performed separately for each year on the data for each trait of interest (yield, plant height, maturity, seed size, lodging) using SAS PROC MIXED (SAS Institute, 1999). Entries were treated as fixed, and location, replication within location, and location by entry were treated as random. The LSMEANS statement with a PDIFF option was used to obtain means for lines, and the standard error of a difference between two means. This standard error was used to calculate a least significant difference (LSD) value for comparing lines at significance level 0.05.

To test for a linear relationship between yield and homozygosity, a mixed model ANOVA was performed on the yield data, combined over years, separately for Cross 1 and Cross 2. Yields for parents were included, and the design was unbalanced with respect to year and entry because in a given year, only a subset of the generations was tested. The linear regression on percentage inbreeding (coded as 0, 50, 75, 87.5, and 93.75 for the F_1, F_2, F_3, F_4, and F_5 generations, respectively) was obtained using an estimate statement with appropriate coefficients for the generation means and coefficients equal to 0 for the parents. The Kenward option (Kenward and Roger, 1997) was used to compute degrees of freedom. This analysis was repeated on the data for the other traits.

RESULTS

Since the breeding objective with a self-pollinated species is usually to select a pure line that is more productive than either parent, high-parent heterosis is of more interest and relevance than mid-parent heterosis. In this experiment, the differences in productivity of both parental pairs were not statistically significant (Table 1 and 2). Thus, mid-parent and high-parent usage of the term heterosis would be similar. For the remainder of this paper usage of the term heterosis will refer to high parent heterosis only.

In both years that the F_1 generations were tested, they yielded more than the highest yielding of their respective parents (Table 1 and 2). The average yield of the Cross 1 F_1 was 16% greater than the high parent (3417 vs. 2940 kg ha^{-1}), and the average yield of the Cross 2 F_1 was 5% greater than the high parent (3185 vs. 3036 kg ha^{-1}). A regression of generation means on the percentage inbreeding in each generation showed a linear decline in yield as inbreeding increased for both crosses, $b = -5.73 \pm 1.36$ kg ha^{-1} ($P < 0.0001$) for Cross 1 and $b = -2.79 \pm 1.65$ kg ha^{-1} ($P = 0.098$) for Cross 2. The completely inbred generation (F_∞) derived from Cross 1 was predicted to yield 573 kg ha^{-1} less than the F_1, a 16.6% decrease. For Cross 2, the F_∞ generation was predicted to yield 2728 kg ha^{-1}, a 9% decline. Thus, while both crosses produced heterosis for yield and inbreeding depression, they were statistically significant for only Cross 1. With bulk selfing, one suspects that lines of descent are not represented equally in the bulked generations. But if this is the case, there would most likely be an upward bias in yield as those lines that produce more seeds would contribute more to the generation mean. Thus, our estimates of inbreeding depression may

Table 1. Yield and seed size of parents, F_1, and inbred generations from Cross 1 (Hutcheson $\times$ Holladay) averaged over locations in each year.†

Generation	Yield				Seed size			
	1999	2000	2001	2004	1999	2000	2001	2004
	kg ha^{-1}				mg seed^{-1}			
F_1	3045	–	3789	–	157	–	157	–
F_2	2671	3217	3305	3383	154	163	155	166
F_3	–	2950	3197	2940	–	156	149	159
F_4	–	–	3442	3036	–	–	147	151
F_5	–	–	–	2856	–	–	–	151
Hutcheson	2461	2927	3130	2804	139	155	152	162
Holladay	2790	2943	3091	2876	148	147	145	142
LSD$_{.05}$	316	361	357	362	11	9	7	7

† Three replications at Clayton, Plymouth, and Windblow, NC in 1999; three replications at Clayton, Plymouth, and Clinton, NC in 2000 and 2001; three replications at Clayton and Plymouth, NC in 2004.

Table 2. Yield and seed size of parents, F_1, and inbred generations from Cross 2 (Brim $\times$ Boggs) averaged over locations in each year.†

Generation	Yield				Seed size			
	1999	2000	2001	2004	1999	2000	2001	2004
		kg ha^{-1}				mg seed^{-1}		
F_1	2858	–	3511	–	142	–	130	–
F_2	2841	2962	3283	2715	143	140	128	145
F_3	–	2798	3164	2493	–	144	127	146
F_4	–	–	3311	2265	–	–	132	138
F_5	–	–	–	2370	–	–	–	148
Brim	2765	2896	3307	2446	131	143	120	132
Boggs	2567	2795	3288	2079	137	136	136	136
LSD$_{.05}$	471	339	429	858	14	6	9	30

† Three replications at Clayton, Plymouth, and Windblow, NC in 1999; three replications at Clayton, Plymouth, and Clinton, NC in 2000 and 2001; three replications at Clayton and Plymouth, NC in 2004.

be smaller than they would have been if each F_2 plant had contributed the same number of seeds to the F_3 bulk generation, each F_3 family, and contributed equally to the F_4 generation, etc. Results were not influenced by genotype $\times$ environment interaction, as neither genotype $\times$ year nor genotype $\times$ location (year) were significant in the combined analysis of yield data from all years.

The other traits that exhibited F_1 heterosis and inbreeding depression were seed size (Table 3) in Cross 1 and lodging in Cross 2 (Table 4). The linear estimate from regression of seed size on percentage inbreeding was $-0.15 \pm .05$ mg seed^{-1}. The linear estimate from regression of lodging on percentage inbreeding was 0.0024 ± 0.0017. As lodging decreased so did yield. Yield decreases in soybean are sometimes accompanied by decreases in lodging. For the traits of maturity and plant height, coefficients from regression of generation means on percentage heterozygosity were nonsignificant. Thus, F_1 yield increases were not due to taller plants, changes in maturity, or decreased lodging. Yield heterosis was most likely due to a greater number of seeds, and in Cross 1 somewhat larger seeds as well.

There was no F_1 heterosis for seed composition traits. Concentrations of protein and oil in the F_1 of both crosses were equivalent to the respective mid-parents (Table 3 and 4).

DISCUSSION

Early quantitative genetic investigations with soybean found significant additive $\times$ additive epistasis for yield (Brim and Cockerham, 1961; Hanson et al., 1967). Because inbreeding depression was rarely observed, one could attribute most heterosis to additive $\times$ additive

epistasis. In our study and others (Brim and Cockerham, 1961; Lewers et al., 1998; Rahangdale and Rout, 2002) finding statistically significant and substantial inbreeding depression is clear evidence that dominance effects are important in some breeding populations. The coefficient of parentage (CP) between the two parental combinations used by Brim and Cockerham (1961), N48–4860/Lee and Roanoke/Lee, were zero. Lee, released in 1950 (Johnson, 1958), was the first cultivar adapted to seed production in the southeast developed through breeding. Roanoke was a 1945 selection from a plant introduction (Weiss, 1953), and N48–4860 was a breeding line developed in 1948. By contrast, in our study, Hutcheson and Holladay had a CP of 0.147 and were released in 1987 and 1993, respectively. Brim and Boggs had a CP of 0.173 and were released in 1997 and 1990, respectively. Yet in both studies, heterosis and the rates of inbreeding depression were significant. Manjarrez-Sandoval et al. (1997) investigated heterosis in F_2 bulks of 24 biparental crosses with coefficients of parentage (CP) between 0.027 and 0.714. They found that neither CP nor genetic similarity estimates based on restriction fragment length polymorphism (RFLP) analysis were predictive of favorable combinations for yield heterosis. Obviously heterosis requires genetic dissimilarity; however, these studies show that genetic dissimilarity alone is a poor predictor of heterosis. Neither, it would seem, is the degree of pure line improvement a predictor of heterotic performance or the lack thereof. Historical studies of maize improvement also have shown no evidence that heterosis has decreased as inbred lines have been improved (Coors, 1999).

In both our study and the Brim and Cockerham study (1961), the predictions for average performance of the

Table 3. Maturity, height, lodging, and concentrations of seed protein and oil of parents, F_1, and inbred generations from Cross 1 (Hutcheson $\times$ Holladay), averaged over locations in 1999 and 2001.†

Generation	Maturity (date)		Height		Lodging (score)		Protein		Oil	
	1999	2001	1999	2001	1999	2001	1999	2001	1999	2001
			mg seed^{-1}				g kg^{-1}		g kg^{-1}	
F_1	10/11	10/11	30	28	2.2	1.3	402	379	198	213
F_2	10/10	10/11	28	25	2.4	1.3	400	385	199	212
F_3	–	10/12	–	28	–	1.4	–	381	–	211
F_4	–	10/11	–	26	–	1.7	–	382	–	213
Hutcheson	10/13	10/10	29	24	2.3	1.2	413	385	193	217
Holladay	10/10	10/9	26	24	2.4	1.2	384	371	199	215
LSD$_{.05}$	2	2	2	3	0.3	0.4	7	10	5	5

† Three replications at Clayton, Plymouth, and Windblow, NC in 1999; Three replications at Clayton, Plymouth, and Clinton, NC in 2001.

Table 4. Maturity, height, lodging, and concentrations of seed protein and oil of parent, F_1, and inbred generations from Cross 2 (Brim $\times$ Boggs), averaged over locations in 1999 and 2001.†

Generation	Maturity (date) 1999	Maturity (date) 2001	Height 1999	Height 2001	Lodging (score) 1999	Lodging (score) 2001	Protein 1999	Protein 2001	Oil 1999	Oil 2001
			cm				g kg⁻¹		g kg⁻¹	
F_1	10/17	10/18	39	37	2.8	2.6	442	395	183	200
F_2	10/15	10/18	37	36	2.9	2.2	435	394	185	198
F_3	–	10/20	–	39	–	2.2	–	395	–	199
F_4	–	10/21	–	36	–	2.1	–	393	–	201
Brim	10/17	10/24	37	37	2.8	2.3	435	395	183	204
Boggs	10/16	10/24	30	33	2.6	2.4	428	388	191	204
LSD.₀₅	2	7	3	3	0.5	0.5	15	10	9	4

† Three replications at Clayton, Plymouth, and Windblow, NC, in 1999; three replications at Clayton, Plymouth, and Clinton, NC in 2001.

totally inbred generations were not significantly different from the mid-parent in any of the four crosses. This prediction may be a reason that inbreeding depression in soybean is disregarded. It is often the experience of soybean breeders that the mean yield of two parents and the mean yield of the pure lines derived from them are equivalent. But nonsignificant deviation of the inbred population mean from the mid-parent does not necessarily imply that dominance is also nonsignificant. The two-locus theory developed by Weir and Cokerham (1977) shows the mean of the completely inbred population to be equivalent to the non-inbred population mean plus a sum of homozygous dominance effects at the two loci, the dominance × dominance interaction of those effects, and a term that is the product of the initial linkage disequilibria and the sum of epistatic effects. The population generated from a biparental cross by selfing the F_1 progeny is expected to have significant gene linkage disequilibria. Because the frequencies of all segregating genes are 0.5, homozygous dominance effects would be zero. Thus a difference between the mid-parent and the mean of inbred line derivatives would be evidence for epistasis. However, these effects can be negative or positive and could cancel each other so that the average would be nonsignificant, as it is in the current study.

The classical hypotheses for the genetic basis of heterosis and inbreeding depression, overdominance, and dominance, have been summarized by Crow (1999). With overdominance, heterozygous alleles interact in a way that results in a significant deviation from the average of the two homozygous genotypes. The dominance hypothesis posits heterozygote advantage as due to complete or incomplete dominance of one allele over another. While neither theory has been proven or disproven, experimental results in plants usually fit a dominance interpretation instead of overdominance (Lamkey and Edwards, 1999; Charlesworth and Charlesworth, 1999). Inbreeding depression with overdominance would be due to loss of heterozygosis per se and with dominance due to an increase in the frequency of homozygous unfavorable (or deleterious) alleles. Interaction of alleles at different loci (epistasis) can also contribute to heterosis. But in a quantitative genetic context, only dominance and dominance-by-dominance effects contribute to inbreeding depression where gene frequencies are 0.5, as they were in the current study (Holland, 2001). Nonlinearity of response to inbreeding generally is considered to be evidence of significant dominance-by-dominance epistasis. But, as we found no significant deviations from linearity in our experiment, dominance-by-dominance effects seem not to have been important or negative and positive effects tended to cancel each other out.

In self-pollinated crop species like soybeans, genetic load should be minimal. Natural selection and/or plant breeding would be expected to eliminate deleterious gene mutations with large effects (Husband and Schemske, 1996). Therefore, the inbreeding depression observed in the current and other studies is assumed not to be due to homozygous deleterious alleles which are often a major contributor to poor inbred line performance in cross-pollinated species. Even so, the presence of deleterious genes cannot be completely ruled out. It has been demonstrated that duplicate loci contribute to the conservation of mildly deleterious genes or less favorable alleles (Husband and Schemske, 1996), and RFLP mapping investigations have shown that more than 90% of nonrepetitive soybean sequences probably are present in two or more copies (Shoemaker et al., 1996). The four parents in the current study were high-yielding cultivars. If they carried deleterious genes, their effects on phenotype were not obvious. But a duplicate gene at another locus could mask the deleterious effect, if it functioned normally. Thus, an F_1 hybrid between two such parents could have duplicate favorable genes in repulsion phase that are dominant to less favorable alleles. If the two favorable alleles exhibit a complementary interaction, a characteristic of autopolyploids, (Bingham et al., 1994), this might be one source of the heterotic response. In fact, Bingham (1998) with an exposition of historical arguments and experimental evidence in maize and other species, makes a strong case that heterosis is due to linked dominant alleles that are inherited as a unit or chromosome block. In the hybrid, these linkage blocks complement each other by masking less favorable alleles and/or through the interaction of duplicate loci. While linkage, duplicate gene interaction, and gene complementation may be involved, F_1 heterosis in soybean could be due simply to a greater number of dominant (favorable) alleles in the hybrid than in either parent singly. With selfing, the proportion of heterozygous loci declines to 0.5 in the F_2 generation and the importance of dominance generation at each segregating locus declines as well. Similarly, duplicate favorable combinations also decrease with inbreeding and would be another source of depression.

Overdominance cannot be discounted. Suppose alleles at a locus produce similar effects as homozygotes but interact when heterozygous to produce a heterotic response. Birchler et al. (2003) suggest that quantitative traits may be controlled by multiple dosage-dependent regulatory loci, and that heterosis occurs when different alleles present at these loci alter structural gene expression. If so, mean response in inbred generations would not be different from that observed in this study. There is also the intriguing idea that genes at duplicate loci might interact in a similar way to that of a heterozygote (MacKey, 1970). This increases the number of possible allelic interactions (Holland, 2001), and dominant or overdominant effects between duplicate loci would be transformed into additive $\times$ additive effects with inbreeding. There is some evidence for this. In peanut, Isleib et al. (1978) found significant variation for yield and yield components in the F_4 and F_5 generations of a six line half-diallel experiment that was due to specific combining ability. They interpreted this to be due to additive $\times$ additive epistasis. Interlocus effects between duplicate loci (that are similar to allelic dominance effects) could be responsible for significant specific combining ability in later inbred generations. In wheat, Weinhues (1968) was able to select inbred lines from two different biparental crosses that were equivalent in yielding ability to the F_1 in a multi-year study; the F_1s averaged 24 and 10% of the better parent in each combination. While transgressive segregation such as this does not require epistasis, it may have been an important factor.

Studies in soybean where variance components of quantitative traits were estimated have always found that additive variance was the most important component of genetic variance with significant additive-by-additive variance in some cases (Burton, 1987). Most breeding programs use pedigree or modified pedigree selection (Brim, 1966) and are designed to exploit both. The successful improvement of soybean productivity over years (Orf et al., 2004) is good evidence for the usefulness and probable primacy of additive genetic variance in soybean breeding populations. Molecular markers that are associated with an agronomic trait in particular genetic backgrounds, but not others (Orf et al., 1999) is evidence that epistasis is probably important as well and may partially explain why some breeding lines and cultivars are good parents and others are not.

If dominance is also an important source of genetic variation for yield in soybean breeding populations as the current study suggests, then the question becomes one of how to best use that variance for productivity improvement. While using dominance directly in development of F_1 hybrid soybeans for farm production is an intriguing possibility, a good hybrid seed production system is not currently available. Progress toward this goal is being made, particularly in China (Sun et al., 1999), but there have been limited resources and research directed at this problem in the United States (Palmer et al., 2003). Even so, the genetic causes of dominance and epistasis variation that have been suggested above can be fixed in a pure-line cultivar with the ex-

ception of overdominance at single loci. Thus, heterosis should be predictive of good parental combinations. Significant heterosis is still apparent in the F_2 generation as our results and others have shown (Manjarrez-Sandoval et al., 1997; Lewers et al., 1998). Soybean breeders sometimes compare F_2 generation performance with parental performance in replicated yield trials. Those parental combinations that show F_2 heterosis are given priority for additional inbreeding and selection (C.N. Tinius, personal communication, 2000; Cooper, 1990). Results from this procedure have been mixed (Weis et al., 1947; Leffel and Hanson, 1961; Reese et al., 1988). But, no studies have been done with soybean to compare the success of line selection from heterotic crosses vs. nonheterotic crosses. When this was done in wheat, the correlation coefficient between F_1 or F_2 bulk performance and the highest yielding 25% of F_5 lines were 0.56 and 0.77, respectively (Cregan and Busch, 1977). Test crossing may be useful. Breeding lines and/or cultivars that are known to have very good combining ability could be used as testers to discover those cross combinations which exhibit heterosis. The procedure suggested by St. Martin et al. (1996) would be useful for this purpose. Also, half-sib recurrent selection methods can be devised to improve population performance and specific combining ability with a particular tester (Feng et al., 2004).

The existence of significant nonadditive gene effects will also influence decisions about the usefulness of early generation selection. In simulation studies, Snape and Riggs (1975) compared the F_2 distribution with the distribution of F_6 lines derived by single-seed descent. They simulated a self-fertilizing diploid with two alleles at each of 21 loci with equal effects on a single trait and four different genetic models: (1) only additive effects, (2) additive effects plus complete dominance for increasing alleles, (3) additive effects plus complete dominance and complementary gene interactions, and (4) additive effects plus complete dominance and duplicate gene interaction. The F_6 distributions were similar for all four models, but the F_2 distributions that included dominance for increasing alleles and epistasis were skewed toward the higher extreme homozygote. Given this result, it would seem that early generation testing would be quite useful when dominance is significant if it could be done efficiently and economically. It is very difficult to select for yield among single F_2 plants in populations derived from the cross of two adapted parents. But, it may be possible to devise a method for selection of combinations that are heterotic, simultaneously deriving $F_{2:3}$ lines from those selected crosses, and following that with a yield test of those lines in the next season. Pure line development would proceed from selected $F_{2:3}$ lines according to the usual practices of each breeding program. Markers might also be useful in this regard if they could be used to identify F_2 plants that have heterotic gene combinations.

We do not know how extensive dominance is in soybean breeding populations, but heterosis for yield in the F_1 or F_2 is not difficult to find (Palmer et al., 2001). There is no guarantee that heterotic parental combina-

tions will produce higher-yielding pure lines than those that are nonheterotic. Yet, the existence of heterosis would be evidence that superior gene combinations are possible. This, combined with efficient selection in the F_2 and/or F_3 generation, might produce a higher frequency of high-yielding pure lines than breeding methods that ignore the possibility of dominance.

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